How carefully executed network theory informs invasion ecology

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In a recent contribution to TREE, Hui and Richardson [1] (H&R) argue that the ecology of open dynamic networks should play a more prominent role in informing invasion ecology. Unfortunately, inaccuracies in the mathematical example they present to illustrate this point led to conclusions that are difficult to support upon closer inspection, including those based on application of May's stability theory in this context (Supplementary Material). But their central point remains valid. Indeed, there are several known results from network ecology that directly respond to questions raised by H&R. Here we give examples addressing: the responses of resident populations to invaders, mechanisms determining invasibility, and the relative importance of habitat and host community in determining invasion success.

Ecological network theory becomes particularly powerful a tool to inform invasion ecology if we focus our attention on ecological communities where structural instability is limiting species richness. These communities are so sensitive to perturbations that each new invasion leads to extinction of one other species on average [2, 3]. How general this phenomenon is remains a matter of discussion [4], but several lines of evidence suggest that for open, local communities such saturation may be common [3, 5–7]. Most theory in this context considers the limit, as we shall here, that the time between invasions is long compared to population-dynamical relaxation times.

H&R ask how large the minimum ecological network is that is required to reliably predict invader impacts. Because structural instability of ecological networks results from amplification of complex indirect interactions throughout the network [3, 8], the entire network typically responds to the invasion of a species (network ecology often considers the reverse transition, removal of residents [9, 10], which is very similar). Prediction of these indirect interactions, however, is extremely difficult [8, 9]. In food-web simulations, only direct predator-prey interactions are reliably predicted [9, 10]. In practice the reasonable network to model therefore includes only direct interaction partners of invaders.

In a statistical sense, predictability can be stronger. Consider a simple Lotka–Volterra competition model where all intraspecific competition coefficients are 1 and interspecific coefficients are independent

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random numbers with mean $\overline{\alpha}$ and variance $\operatorname{var}\alpha$. One then finds that, in a large community with S resident species, the vector of changes $\Delta\boldsymbol{\beta}$ in the abundances of residents in response to an invasion event is such that total abundance remains constant on average. In addition, abundances vary apparently at random in response to invasions, such that

$$\operatorname{var}\Delta\boldsymbol{\beta} \approx \frac{\beta_0^2 \operatorname{var}\alpha}{(1-\overline{\alpha})^2 - S\operatorname{var}\alpha} \tag{1}$$

[3, Eqs. (17.11, 17.14, 17.24)], where β_0 is the invader's equilibrium abundance after invasion. The denominator in this expression represents the amplification of perturbations through indirect interactions. When the value of $S\operatorname{var}\alpha$ approaches $(1-\overline{\alpha})^2$, the system responds particularly strongly, signalling the onset of structural instability.

The question to what extent habitat suitability predicts invasion success depends on the size of this effect in comparison with variations in invasion fitness [1, 11] contingent on biotic interactions with residents. Habitat suitability will not play a notable role if its effect on fitness is small compared to the standard deviation $\mathrm{SD}(r)$ of invasion fitness r due to biotic interactions. So, how large is $\mathrm{SD}(r)$? For a Lotka–Volterra competition model of a saturated open community, with richness fluctuating around S species, where the monoculture linear growth rate at low density has the same value s for all species and interspecific competition coefficients are independent and identically distributed as above,

$$\mathrm{SD}(r) \approx \frac{1-\overline{\alpha}}{1.3\,S\,\overline{\alpha}}\,s \tag{2}$$

[3, Eqs. (17.8), (17.26)]. Equation (2) is remarkable because its parameters can easily be estimated empirically. Imagine a community of $S = 20$ competing species where, on average, population sizes are 1/4 of their monoculture carrying capacity, so $1/[1+(S-1)\overline{\alpha})] = 1/4$, implying $\overline{\alpha} = 3/19$. Hence, by Eq. (2), $\mathrm{SD}(r) \approx 0.2\,s$. Fitness differences due to habitat suitability predict invasion success only if they are at least of a similar magnitude.

Finally, a central topic that H&R discuss is community invasibility [11], i.e. *the probably that a random species can invade*. In saturated communities, the following constraints determine invasibility:

1. Typically, species persist in a community if and only if they can invade when rare.

2. Species are to some degree filtered by their host community at the time they invade, but once they are residents and the host community continues to turns over, it becomes gradually randomised from the residents' perspective.

3. The rate of extinction of residents equals the rate of random invasions driving turnover.

Constraints 1 and 2 combined imply that the number of extinctions per invasion decreases with increas-

ing invasibility. Constraint 3 then determines a specific value for invasibility. For communities with asymmetric random competition one finds that *independent of model parameters and other details*, the resulting invasion probability is approximately 1/2 [3, Sec. 14.6], in agreement with simulations [3, 11] and observations for vertebrates [12]. For communities with some correlation between pairwise competition coefficients (as expected for plants), similar calculations show that invasibility will be lower [3, Sec. 17.3].

While requiring further development, in particular to fully incorporate effects of correlated competition coefficients, these results indicate avenues for achieving the tighter synthesis between network- and invasion ecology that H&R advocate.

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Supplementary Material

for

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by

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1 Technical critique of the theory for stability to invasion by Hui and Richardson

Hui and Richardson (H&R) [1] present the interesting idea that population growth rates of potential invaders and the initial responses of resident populations to invasions are given respectively by the eigenvalues and eigenvectors of the Jacobian matrix $\mathbf{J}$ of the pre-invasion equilibrium community state (assuming such an equilibrium is reached), provided the population sizes of potential invaders are included as dynamic variables in the model. To pinpoint inaccuracies in the reasoning of H&R that concern us, we state here a theorem characterising generic aspects of population dynamics implied by H&R's idea.

Notation: For any $n, m > 0$ and any n-component vector of real or complex numbers $\mathbf{v}$ we denote by $\mathrm{diag}(\mathbf{v})$ the $n \times n$ diagonal matrix with diagonal entries given by the entries of $\mathbf{v}$. Further, as conventional, we denote by t the time variable of a dynamical system, by $\mathbb{R}$ the set of all real numbers, and by $\mathbb{R}^n$ and $\mathbb{R}^{n\times m}$ respectively the sets of all real-valued vectors of size n and real-valued matrices of size $n \times m$.

Theorem 1. *Let S' and S'' be positive integers, $S = S' + S''$, and the function $\mathbf{f} : \mathbb{R}^S_{\geq 0} \to \mathbb{R}^S$ be differentiable over its domain. Assume that the system of ordinary differential equations*

$$\frac{d\mathbf{N}}{dt} = \mathrm{diag}(\mathbf{N})\mathbf{f}(\mathbf{N}) \tag{1}$$

has an equilibrium $\mathbf{N}(t) \equiv \mathbf{N}^* = (N_1^*, ..., N_S^*)^{\mathrm{T}} \in \mathbb{R}^S_{\geq 0}$ such that $N_1^*, ..., N_{S'}^* > 0$ and $N_{S'+1}^*, ..., N_S^* = 0$. Denote by $\mathbf{r}$ the S''-component vector given by the last S'' components of $\mathbf{f}(\mathbf{N}^*)$. Then the following holds:

1. *The first S' components of $\mathbf{f}(\mathbf{N}^*)$ are zero, i.e. $\mathbf{f}(\mathbf{N}^*)$ has the $(S' + S'')$-block form $\mathbf{f}(\mathbf{N}^*) = \binom{0}{\mathbf{r}}$.*
2. *The Jacobian matrix $\mathbf{J}$ of system (1) at $\mathbf{N} = \mathbf{N}^*$ is of the $(S' + S'') \times (S' + S'')$-block form*

$$\mathbf{J} = \begin{pmatrix} \mathbf{J}' & \mathbf{J}'' \\ 0 & \mathrm{diag}(\mathbf{r}) \end{pmatrix}, \tag{2}$$

   with some $\mathbf{J}' \in \mathbb{R}^{S'\times S'}$, $\mathbf{J}'' \in \mathbb{R}^{S'\times S''}$.
3. *The set of eigenvalues of $\mathbf{J}$ equals the union of the set of eigenvalues of $\mathbf{J}'$ and the set given by the elements of $\mathbf{r}$.*
4. *Let $\mathbf{J}$ have S distinct eigenvalues (i.e. all eigenvalues have multiplicity one). Then eigenvectors belonging to eigenvalues of $\mathbf{J}$ that are also eigenvalues of $\mathbf{J}'$ have zeros in their last S'' elements, and eigenvectors belonging to eigenvalues that are elements of $\mathbf{r}$ have exactly one non-zero value among the last S'' elements.*

Nothing stated in the theorem is original from a mathematical perspective, yet we provide an elementary proof in Section 2 below.

We observe that Fig. 1B of H&R is at odds with the second statement of the theorem, their Fig. 1C and its interpretation contradict the theorem's third statement, and their Fig. 1D is inconsistent with the fourth statement. Most importantly, *interactions amongst residents and between residents and invaders have no effect on the population growth rates of potential invaders when interaction strengths are understood as being given by the entries of* $\mathbf{J}$. The growth rates of potential invaders are given exclusively by the diagonal elements of $\mathbf{J}$ that would, by this understanding, represent the invaders' "self-interaction strengths". This undermines many of the wider conclusions that H&R draw building on May's stability theory [2].

Central to our analysis is the observation that, to accommodate the principle of biological reproduction, the relevant generic model for the dynamics of $\mathbf{S}$ interacting populations $N_1, \ldots, N_S$ is not $\frac{dN_i}{dt} = F_i(N_1, \ldots, N_S)$, with a generic smooth functions F_i $(1 \leq i \leq S)$, assumed by H&R, but the more constrained model $\frac{dN_i}{dt} = N_i f_i(N_1, \ldots, N_S)$ with smooth functions f_i representing momentary linear population growth rates. The theorem addresses community equilibria where $N_i = 0$ for potential invaders i. If one were instead to study the equilibria with small $N_i > 0$ occurring with strong Allee effects, corrections to our results would arise. Qualitatively, the resulting picture would then conform better with that developed by H&R. Quantitatively, however, we'd expect the corrections to be generally small in comparison with the characteristics derived here.

2 Proof of Theorem 1

The proofs for the four numbered statements of Theorem 1 are given in the order stated, following the same numbering. Throughout we denote by $f_i(\mathbf{N})$ the i-th component of the value of the function $\mathbf{f}(\mathbf{N})$, by r_n the n-th element of $\mathbf{r}$, and similarly for other vectors.

1. By assumption, Eq. (1) has an equilibrium at $\mathbf{N}^*$, i.e., $\mathrm{diag}(\mathbf{N}^*)\mathbf{f}(\mathbf{N}^*) = 0$. The i-th component $(1 \leq i \leq S)$ of this equation is

$$N_i^* f_i(\mathbf{N}^*) = 0. \tag{3}$$

   This is satisfied if $N_i^* = 0$ or $f_i(\mathbf{N}^*) = 0$. For the first S' components $(1 \leq i \leq S')$, $N_i^* > 0$ by assumption of the theorem, hence $f_i(\mathbf{N}^*) = 0$. Therefore the first S' components of $\mathbf{f}(\mathbf{N}^*)$ are zero. With $\mathbf{r}$ defined as representing the last S'' components of $\mathbf{f}(\mathbf{N}^*)$, this implies the statement that $\mathbf{f}(\mathbf{N}^*) = \binom{0}{\mathbf{r}}$.

2. Denote by N_k the k-th component of $\mathbf{N}$, and by J_{kl} the matrix element in the k-th row and l-th column of $\mathbf{J}$. The second statement of the theorem does not make any claim about the values in the first S' rows of the Jacobian $\mathbf{J}$. The claim of Eq. (2) regarding the last S'' rows is equivalent to the two claims that, with $S' + 1 \leq k \leq S' + S''$,

   (a) $J_{kl} = 0$ for any $l \neq k$ $(1 \leq l \leq S)$ and

   (b) $J_{kk} = f_k(\mathbf{N}^*)$.

   To verify these two claims, first recall that, by definition,

$$J_{kl} = \left.\frac{\partial(dN_k/dt)}{\partial N_l}\right|_{\mathbf{N}=\mathbf{N}^*}. \tag{4}$$

   Inserting Eq. (1), applying the chain rule for differentiation of products, and then invoking the assumption of the theorem that $N_k^* = 0$ for $S' + 1 \leq k \leq S' + S''$, this becomes

$$\begin{aligned} J_{kl} &= \left.\frac{\partial[N_k f_k(\mathbf{N})]}{\partial N_l}\right|_{\mathbf{N}=\mathbf{N}^*} \\ &= \left.\frac{\partial N_k}{\partial N_l}\right|_{\mathbf{N}=\mathbf{N}^*} f_k(\mathbf{N}^*) + N_k^* \left.\frac{\partial f_k(\mathbf{N})}{\partial N_l}\right|_{\mathbf{N}=\mathbf{N}^*} \\ &= \left.\frac{\partial N_k}{\partial N_l}\right|_{\mathbf{N}=\mathbf{N}^*} f_k(\mathbf{N}^*). \end{aligned} \tag{5}$$

   When $l \neq k$ the variables N_l and N_k are different and so $\partial N_k/\partial N_l = 0$. The last line of Eq. (5) therefore evaluates to zero, implying $J_{kl} = 0$ and proving claim (a). For $l = k$, we have $\partial N_k/\partial N_l = \partial N_k/\partial N_k = 1$. Equation (5) then become $J_{kk} = f_k(\mathbf{N}^*)$, confirming claim (b). This concludes the proof of the second statement of the theorem.

To prove statements 3 and 4 of the theorem, it is useful to write the eigenvalue problem

$$\mathbf{J}\mathbf{v} = \lambda\mathbf{v}, \tag{6}$$

with $\mathbf{J}$ given by Eq. (2), complex-valued λ and $\mathbf{v}$, and $|\mathbf{v}| \neq 0$, as

$$\mathbf{J}'\mathbf{v}' + \mathbf{J}''\mathbf{v}'' = \lambda\mathbf{v}' \tag{7a}$$
$$\mathrm{diag}(\mathbf{r})\mathbf{v}'' = \lambda\mathbf{v}'', \tag{7b}$$

splitting the eigenvector $\mathbf{v}$ into two blocks $\mathbf{v} = \binom{\mathbf{v}'}{\mathbf{v}''}$. In the following, two types of solutions of this problem will be distinguished. Type I are solutions where the last S'' elements of $\mathbf{v}$ are all zero, i.e. $\mathbf{v}'' = 0$. Type II are solutions where at least one of the last S'' elements of $\mathbf{v}$ is non-zero, i.e. $|\mathbf{v}''| \neq 0$. Clearly, any solution of Eq. (7) is either of Type I or Type II.

3. To prove the third statement, it needs to be shown that

   (A) all eigenvalues of $\mathbf{J}$ are eigenvalues of $\mathbf{J}'$ or elements of $\mathbf{r}$,

   (B) any number λ that is an eigenvalue of $\mathbf{J}'$ is also an eigenvalue of $\mathbf{J}$, and

   (C) any number λ that is an element of $\mathbf{r}$ is an eigenvalue of $\mathbf{J}$.

   We begin with (A). For any eigenvalue of $\mathbf{J}$, there is a corresponding eigenvector $\mathbf{v}$ solving Eq. (6). For solutions of Type I (where $\mathbf{v}'' = 0$), Eq. (7a) reduces to $\mathbf{J}'\mathbf{v}' = \lambda\mathbf{v}'$. Eigenvalues of $\mathbf{J}$ pertaining to these solutions are therefore also eigenvalues of $\mathbf{J}'$, consistent with (A). For solutions of Type II, denote by n the index of a non-zero element of $\mathbf{v}''$. The n-th line of Eq. (7b) then reads

$$r_n v''_n = \lambda v''_n. \tag{8}$$

   Because $v''_n \neq 0$, the equation implies $\lambda = r_n$, i.e. the eigenvalue is an element of $\mathbf{r}$, also in agreement with statement (A). Because (A) holds for both Type I and Type II eigenvectors, it holds for all eigenvectors and so all eigenvalues of $\mathbf{J}$.

   Next we prove (B). Let λ be an eigenvalue $\mathbf{J}'$. Then there is a corresponding eigenvector $\mathbf{v}' \neq 0$ solving $\mathbf{J}\mathbf{v}' = \lambda\mathbf{v}'$. To confirm that λ is also an eigenvalue of $\mathbf{J}$, let $\mathbf{v} = \mathbf{v} = \binom{\mathbf{v}'}{\mathbf{v}''}$ with $\mathbf{v}'' = 0$. Putting this into Eq. (7) one sees that λ and $\mathbf{v}$ solve the eigenvalue problem for $\mathbf{J}$, as stated under (B).

   Finally, to prove (C), let n be the index of an element of $\mathbf{r}$ that equals λ, i.e., $r_n = \lambda$. If λ is also an eigenvalue of $\mathbf{J}'$, existence of a corresponding eigenvector of $\mathbf{J}$ was already shown under (B), so this possibility can be excluded in the following. An eigenvector of $\mathbf{J}$ corresponding to eigenvalue λ can then be constructed as follows. Choose $\mathbf{v}'' \in \mathbb{R}^{S''}$ as the vector whose n-th element is 1 and whose other elements are 0. With this $\mathbf{v}''$, Eq. (7b) is satisfied: the n-th component of Eq. (7b) is $r_n = \lambda$, which is satisfied by the choice of r_n, and all other components evaluate to $0 = 0$. Equation (7a) is equivalent to $(\mathbf{J}' - \lambda\mathbf{I}_{S'})\mathbf{v}' = -\mathbf{J}''\mathbf{v}''$, with $\mathbf{I}_{S'}$ denoting the $S' \times S'$ identity matrix. The eigenvalues of the matrix $(\mathbf{J}' - \lambda\mathbf{I}_{S'})$ are given by subtracting λ from the eigenvalues of $\mathbf{J}'$ (with identical eigenvectors). Cases where λ is an eigenvalue of $\mathbf{J}'$ were treated separately above. For the remaining cases zero is not an eigenvalue of $(\mathbf{J}' - \lambda\mathbf{I}_{S'})$. Hence $(\mathbf{J}' - \lambda\mathbf{I}_{S'})$ is non-singular and invertible, and Eq. (7a) uniquely solved by choosing

$$\mathbf{v}' = -(\mathbf{J}' - \lambda\mathbf{I}_{S'})^{-1}\mathbf{J}''\mathbf{v}''. \tag{9}$$

   The combined vector $\mathbf{v} = \binom{\mathbf{v}'}{\mathbf{v}''}$ is then an eigenvector of $\mathbf{J}$ and $\lambda = r_n$ the corresponding eigenvalue, which was the claim of (C).

4. To prove the fourth statement, write $\mathbf{v} = \binom{\mathbf{v}'}{\mathbf{v}''}$ as above. The S'' last equations of the eigenvalue problem for $\mathbf{J}$, Eq. (7b), can then be written as

$$(r_i - \lambda)v''_i = 0 \qquad (1 \leq i \leq S''). \tag{10}$$

   This equation is satisfied if $(r_i - \lambda) = 0$ or $\mathbf{v}''_i = 0$. Because, by the third statement of the theorem, all eigenvalues of $\mathbf{J}$ are eigenvalues of $\mathbf{J}'$ (of which there are at most S') or elements of $\mathbf{r}$ (of which there are at most S''), the assumption of the fourth statement that all $S = S' + S''$ eigenvalues are different implies that $\mathbf{J}'$ has S' different eigenvalues and that all S'' elements of $\mathbf{r}$ are different from each other and from the eigenvalues of $\mathbf{J}'$. Hence, if λ is an eigenvalue of $\mathbf{J}'$ it cannot equal an element of $\mathbf{r}$, implying that $(r_i - \lambda) \neq 0$ and $v''_i = 0$ for all i, thus confirming that $\mathbf{v}'' = 0$. If, on

the other hand, λ equals an element of $\mathbf{r}$, say, the n-th element, then $(r_n - \lambda) = 0$, implying that v''_n may be non-zero. And because $r_i \neq \lambda = r_n$ for $i \neq n$, the other $S'' - 1$ elements of $\mathbf{v}''$ must be zero by Eq. (10). It remains to be demonstrated that $v''_n \neq 0$. This is best shown by contradiction. Assume that $v''_n = 0$. This implies $\mathbf{v}'' = 0$ and through Eq. (9), which applies for eigenvalues that are elements of $\mathbf{r}$ but not eigenvalues of $\mathbf{J}'$, that $\mathbf{v}' = 0$. Hence $\mathbf{v} = \binom{\mathbf{v}'}{\mathbf{v}''} = 0$. But if $\mathbf{v} = 0$ it can, by definition, not be an eigenvector. Therefore $v''_n \neq 0$. This concludes the proof of the fourth statement of the theorem.

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